CONCENTRATION OF ENVIRONMENTAL EXTREMES AS THE BASIS FOR VEGETATION AREAS

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Concepts of vegetation areas are ordinarily based upon some concept of endemism; that is, a geographical area whose flora contains a noteworthy number of species endemic to that area is thought of as a vegetational unit. These areas are usually given boundaries coinciding with major physiographic features, but the environmental features of the region enter only secondarily into the picture.

In a recent publication based upon a transect study in western and central Oregon (Detling, 1948) attention was called to the correlation existing between the percentage of endemism in the various vegetation belts and the degree of extremeness of environmental factors in those same belts. It was shown that where gradients of several environmental factors exist, those areas where the greatest number of extremes occur are the ones which show the highest percentages of endemism, while those areas along the gradient where the environment is most moderate are characterized by a relatively low degree of endemism.

This being true, it should hold that over any extensive geographical region those centers in which the extremes of a number of climatic or other environmental gradients occur together will be the centers of endemism as regards their flora. This should serve as a basis for dividing such a region into vegetation areas, each with its characteristic flora.

The present paper describes the procedure which has been followed in mapping such areas for the Pacific Northwest, and shows how the areas thus established are related to the distribution of a few of the dominant plant species.

The environmental factors upon which this investigation is based are all climatic features, viz., annual precipitation, average January temperature, average July temperature, and length of the period between the last killing frost in the spring and the first killing frost in the fall. These features in themselves may not always be what are most important as the limiting factors in the distribution of plant species, but they undoubtedly reflect those features which are the limiting factors. Seasonal distribution of rainfall may be of greater importance to plant life in some areas than the annual total, but in the geographical region under consideration the relative distribution of moisture among the seasons is fairly constant, no matter what may be the actual total precipitation. Again, the limiting factor for plants in winter temperatures is the actual lowest temperature that occurs, but it is found in comparing these lowest temperatures where they are available that they

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vary from one locality to another directly as the average January temperature varies, and are thus reflected with sufficient accuracy in these January averages to make the latter valid for purposes of our comparative study.

The data used in this investigation are readily available in the annual reports of the United States Weather Bureau. The climatic maps are adapted from the 1941 Yearbook of the United States Department of Agriculture, "Climate and Man." Data on the climatic features which might have more direct bearing on the flora, such as those just discussed, are not available from a sufficient number of stations over as large an area as the Pacific Northwest, and to collect them would have been a task of too large proportions for one worker to undertake.

Edaphic factors are of great importance in determining the character of a flora. They frequently serve to explain local variations, or in some instances even form the basis for subdividing the major vegetation areas into smaller units, but climate still remains the chief basis upon which these major floras are determined, and for this reason edaphic conditions have not been included in this study.

The first step in the mapping procedure was to determine the gradients for each individual environmental factor. These are shown in the climatic maps of Figures 1 to 4. A cursory inspection of the maps is sufficient to reveal the location of the extremes of these gradients. Examples of extremes, either high or low, may be noted in the annual precipitation in the Olympic Mountains, in the Big Bend of the Columbia River, and at Pyramid Lake in western Nevada, in the average July temperature on the Oregon and Washington coasts, in the Rogue River Valley, and in the Big Bend of the Columbia River, in the average January temperature on the southern Oregon coast, the Cascade Mountain summits, and the lower Clearwater River in Idaho, and in the length of growing season on the southern Oregon coast and on the plateau of central Oregon.

The location of the more noteworthy of the gradient extremes for all four climatic factors is indicated in Figure 5. High extremes of temperatures and precipitation and the longest growing seasons are marked by solid dots, the opposite extremes by circles. The letters accompanying these marks indicate the climatic factors to which they appertain, as follows: P, annual precipitation; S, July (summer) temperature; W, January (winter) temperature; G, growing season.

When the extremes for all factors are mapped together in this manner it is noted that there are certain points around which they tend to be concentrated. According to the findings of the study previously referred to it is at these points that we should expect the highest degree of endemism. The next step, therefore, was to locate the major concentrations of extremes, which would serve as

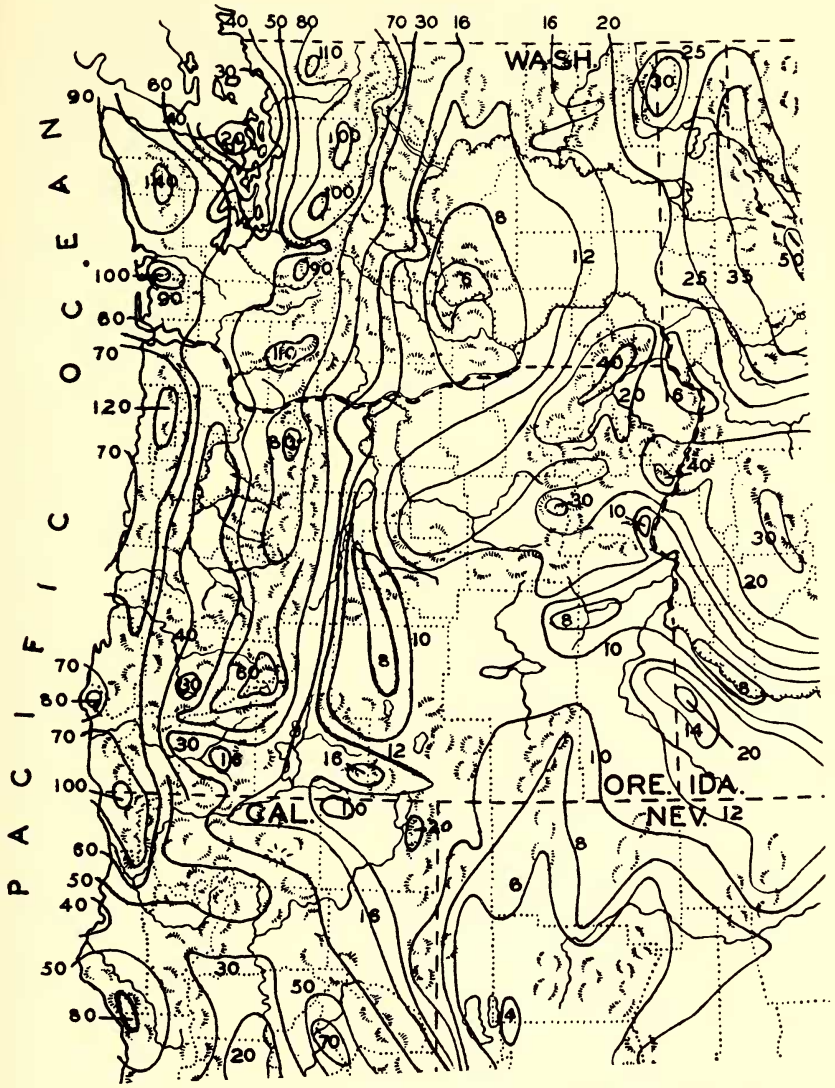

Fig. 1. Annual precipitation in inches in the Pacific Northwest.

the environmental centers of the vegetation areas for the region under consideration. The solid triangles in Figure 6 indicate the location of these centers.

Figure 6 shows, in addition to the environmental centers already mentioned, the limits of the floral areas of the Pacific Northwest. In fixing boundaries for the areas it was assumed that such boundaries should represent as nearly as possible for

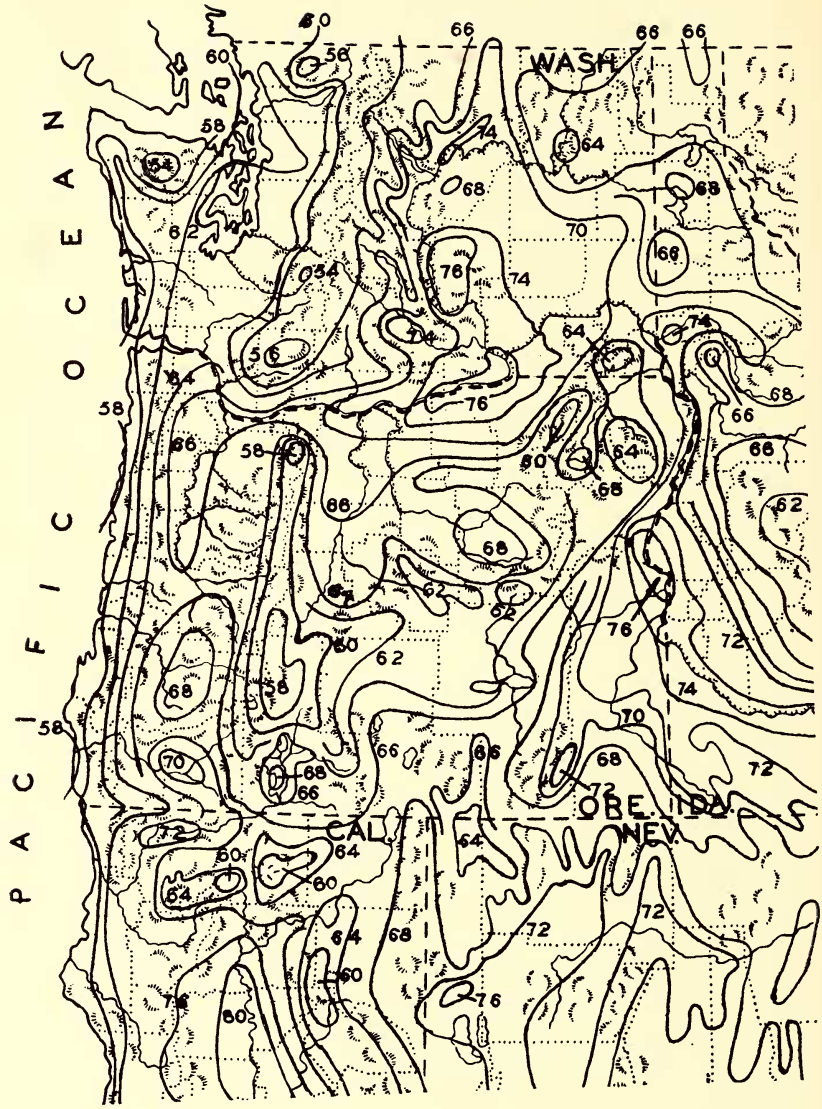

Fig. 2. Average July temperature in °F. in the Pacific Northwest.

each climatic factor the isopleth marking the median point between gradient extremes. Since these isopleths do not coincide for all factors, it was necessary to establish a line which most nearly expressed their average. When so constructed, the boundaries between adjacent areas lie along the lines which are farthest removed from what might be termed the "influence" of their

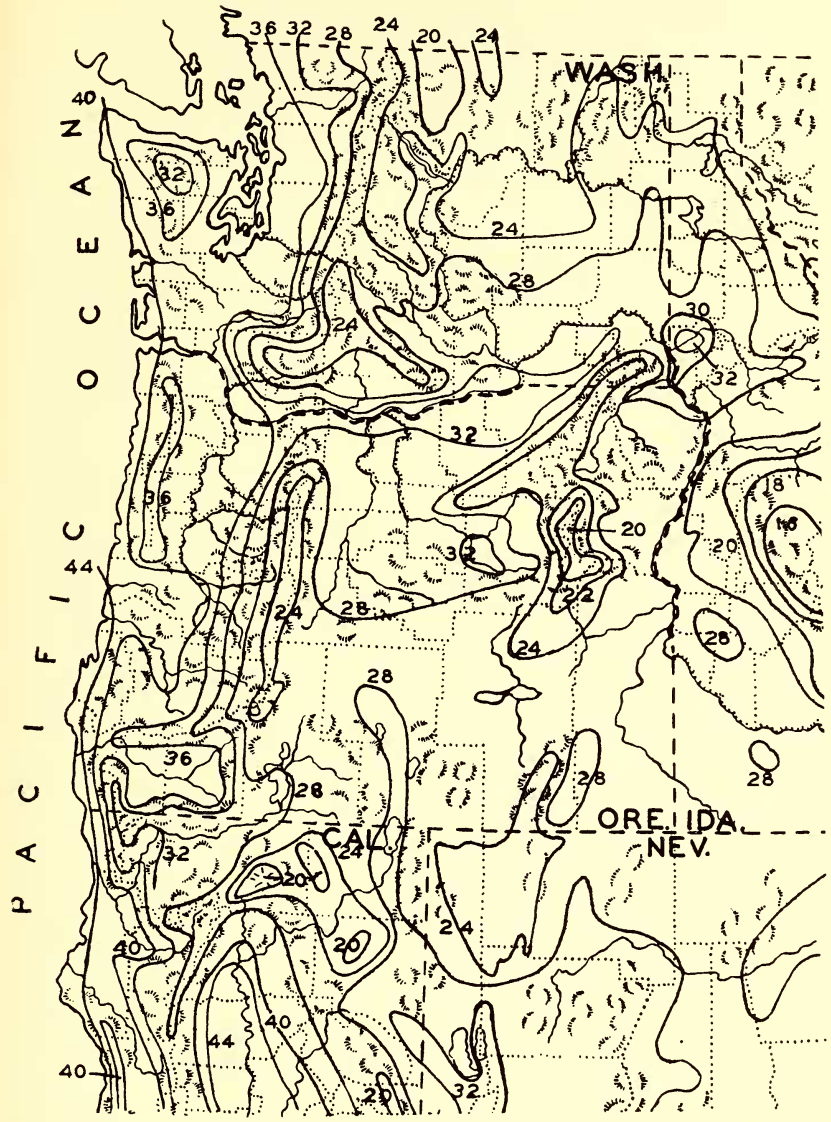

Fig. 3. Average January temperature in °F. in the Pacific Northwest.

respective centers of extremes. In other words, the territory within a vegetation area comprises what is environmentally most closely related to the point of greatest concentration of extremes around which the area is built. The sinuous courses frequently followed by the boundary lines correspond to the courses of some or all of the isopleths upon which they are based.

It should be emphasized that the important thing in each area is its center of environmental extremes, not its boundaries. This center is the center of endemism as well, and the farther we go from this point of greatest influence the less pronounced does endemism become, until at the boundary of the area the flora partakes equally of the characteristics of two adjacent floras.

It will be noted that in some instances more than one area is featured by the same combination of extremes. For example, most of the mountainous areas are characterized by high annual precipitation, low summer and winter temperatures and short growing season. It would seem that such similarity in climate would tend to cause a corresponding similarity in floras. Such areas, however, are always separated from one another by regions in which at least one, and sometimes more, of the climatic factors are at its opposite extreme. These intervening belts, because of this environmental difference, apparently serve as barriers to the migration and consequent mingling of many plant species.

The concept of vegetation areas based upon centers of environmental extremes offers an explanation for a number of features of the distribution of plant species in the Pacific Northwest. The location in western Nevada of the environmental center for the long arm that extends northward into southern Lake and Klamath counties in Oregon explains why so many species listed for the latter locality extend into California and Nevada rather than northward. Similarly, the location on the Columbia River of a center of an environmental unit including north central Oregon and central Washington explains why the flora of north central Oregon is so closely related to that of central Washington and so different from that of south central Oregon. The reason for the sharp break in the coastal flora in the vicinity of Coos Bay, Oregon, becomes evident when one notes the two coastal centers in Del Norte County, California, and near Grays Harbor, Washington. Another interesting question is, "Why is the Coast Range in Oregon a region with so few endemic species?" It will be noted on the climatic maps that there is no striking concentration of extremes in these mountains, a fact which probably accounts for the low degree of endemism. It is this lack of extremes which excludes the Coast Range as a vegetation area in the present scheme, although it has been so considered by other botanical writers.

The Vegetation Areas of the Pacific Northwest

The following summary of the vegetation areas attempts to present briefly the climatic features of each, along with the main floral elements which characterize the area. No attempt is made here to compile an extended list of endemic species, but merely to show the framework for each area, within which a greater or

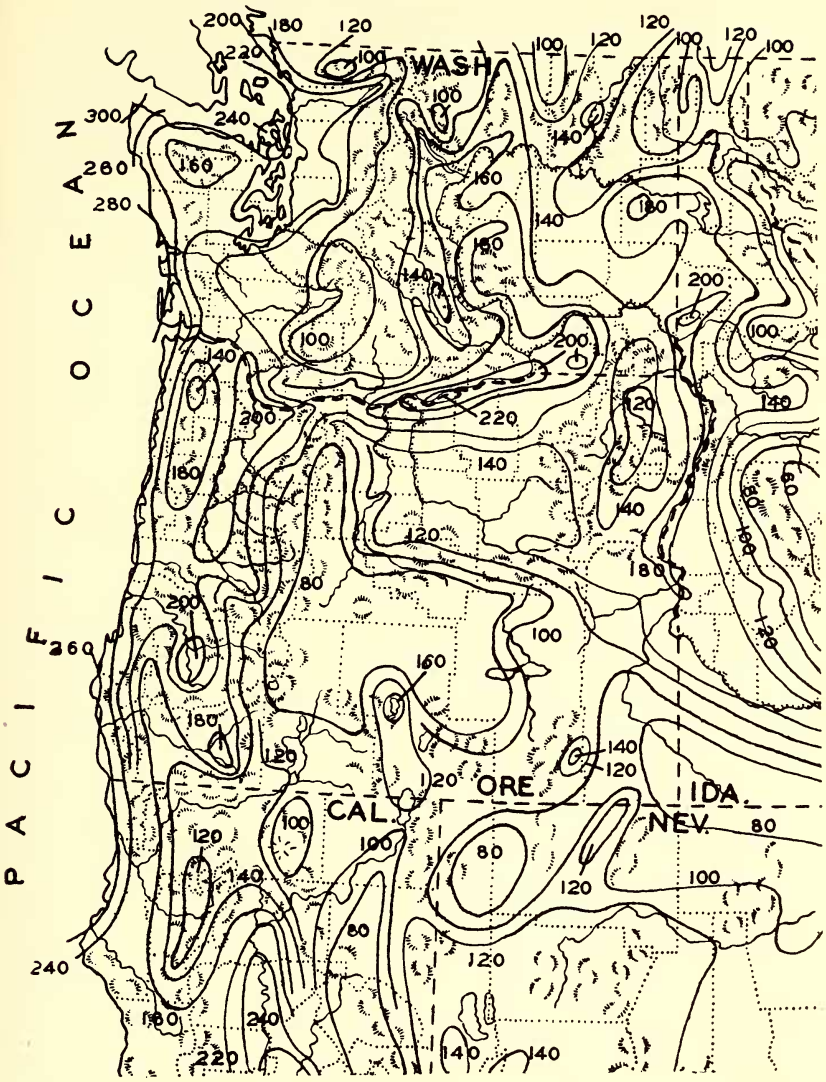

FIG. 4. Average length in days of the growing season in the Pacific Northwest.

lesser number of endemics do occur, as may be ascertained by consulting any manual of the flora of the region.

The names selected for the areas are for the most part those of some geographical feature at or near the environmental center of the area.

The present treatment is limited to those areas occurring either wholly or in part in the states of Washington and Oregon, except

that the Sierra Area has been included because of its close floristic relationship with the areas of southern Oregon.

Del Norte Area. This is a region of high annual precipitation, low summer temperatures, high winter temperatures and long growing season. The dominant species throughout much of the area is *Pseudotsuga taxifolia,* but the two most characteristic tree species are *Sequoia sempervirens* and *Chamaecyparis Lawsoniana.* Other species marking the area are *Umbellularia californica, Lithocarpus densiflora, Quercus chrysolepis, Ceanothus thyrsiflorus,* and *Rhododendron occidentale.*

North Coast Area. The climatic extremes here are the same ones found in the Del Norte Area, the most significant difference lying in the lower winter temperatures occurring in the more northerly area. *Pseudotsuga taxifolia* is again the dominant species, but *Sequoia sempervirens* and *Chamaecyparis Lawsoniana* are replaced by *Picea sitchensis* and notable stands of *Thuja plicata* and *Tsuga heterophylla.*

Olympic Area. This mountain massif, representing the highest elevation lying between the North Coast and Puget Areas, is the center of the extremes of high precipitation, low summer and winter temperatures, and short growing season. The dominant vegetation consists of a forest of *Pseudotsuga taxifolia, Thuja plicata* and *Tsuga heterophylla.* The occurrence of *Abies lasiocarpa, A. amabilis, A. procera, Tsuga Mertensiana* and *Chamaecyparis nootkatensis,* along with those species already named, emphasizes the general similarity of the flora of this area to that of the North Cascade. The Olympic Area, however, lacks the *Picea Engelmannii, Larix Lyallii* and *Pinus albicaulis* of the Cascades, as well as a number of herbaceous species as listed by Piper (1906). On the other hand, a considerable number of herbaceous or shrubby species are endemic to the Olympics.

Siskiyou Area. The mountain massif composed of the Siskiyou and Trinity mountains, marked by a high extreme of precipitation and low extremes of summer and winter temperatures and of growing season, is separated climatically from the similar extremes of the Cascade-Sierra divide by opposite extremes in the lower elevations of the Klamath, Pit and upper Sacramento valleys. The dominant vegetation in the western part of the area (its environmental center) is a *Pseudotsuga* forest mixed with *Lithocarpus densiflora* and *Quercus chrysolepis.* This changes eastward to a forest of *Pinus ponderosa* and *P. Jeffreyi.* The area is one of a high degree of floral endemism, marked by such species as *Pinus Balfouriana, Picea Breweriana, Cupressus MacNabiana, Juniperus californica siskiyouensis, Lithocarpus densiflora echinoides, Quercus Breweri, Q. Sadleriana* and *Q. vacciniifolia.*

Rogue Area. This area is one of relatively low rainfall, high summer temperature, moderate winter temperature, and long growing season. The dominant vegetation is a deciduous wood-

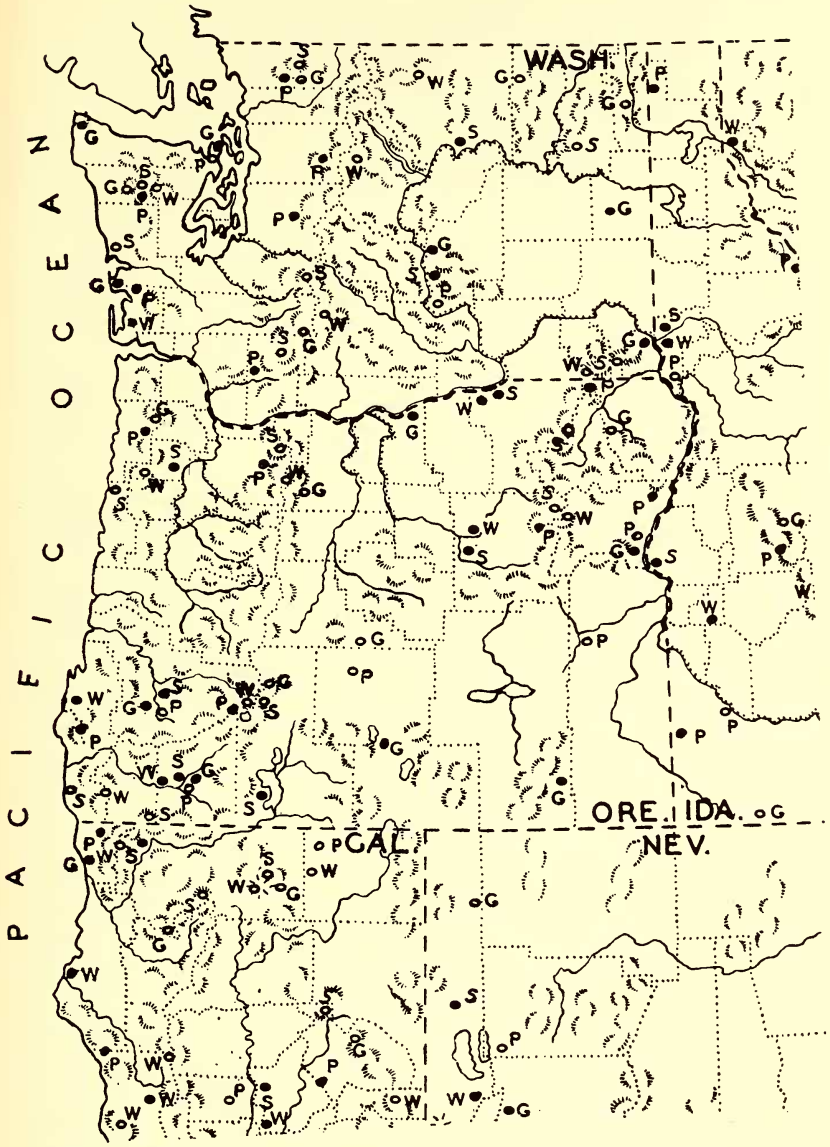

Fig. 5. Principal gradient extremes in the Pacific Northwest for annual precipitation (P), average July temperature (S), average January temperature (W), and length of growing season (G); high ●, low ○.

land consisting of *Quercus Garryana, Q. Kelloggii* and *Arbutus Menziesii,* with a generous mixture of *Pinus ponderosa,* especially on slopes just above the preceding. Important shrubs characterizing the area are *Rhus diversiloba, Ceanothus cuneatus* and *Arctostaphylos viscida.*

Puget Area. The great trough between the Coast Range and the Cascades, extending from Puget Sound southward to the Calapooya Mountains in Oregon, has the same climatic extremes as does the preceding area. However, at its center, on lower Puget Sound, the long growing season extreme is more pronounced than in the Rogue, the high summer temperature extreme is less pronounced, while winter temperatures are about the same. The vegetation of the Puget Area is predominantly the *Pseudotsuga* forest, mingled in cool valleys and on north slopes with *Thuja plicata* and *Tsuga heterophylla,* and in its drier phase with *Arbutus Menziesii* and *Quercus Garryana.* It lacks the *Picea sitchensis* of the adjacent North Coast Area, and the *Quercus Kelloggii* and *Pinus ponderosa* of the Rogue.

North Cascade Area. The high mountains of this area result in a high extreme of precipitation, and low extremes in both winter and summer temperatures as well as in length of growing season. The vegetation at the altitudes where these extremes occur is a subalpine forest consisting of *Tsuga Mertensiana, Abies lasiocarpa* and *Pinus albicaulis,* flanked at lower elevations by *Pinus contorta Murrayana* and *Picea Engelmannii,* and by *Pseudotsuga taxifolia* mixed with *Abies procera* and *A. amabilis.*

South Cascade Area. This area, with climatic extremes similar to those of the preceding one, is separated from it physiographically and climatically by the break in the Cascade Range where the Columbia River cuts through. The plant species dominant in the North Cascade Area are present also in the South Cascade, but the association in the latter is altered by the addition of *Pinus Lambertiana, P. attenuata* and *Abies magnifica* and its variety *shastensis.*

Sierra Area. Geographically and physiographically this area occupies a position similar to that of the North Cascade and South Cascade Areas, and like them is marked by a high extreme of precipitation and low extremes of summer and winter temperature and of growing season. An environmental break at the Pit and Klamath rivers marks the transition from the flora of the South Cascade to that of the Sierra Area. Typical of the vegetation of the latter area are *Pinus Jeffreyi, P. Lambertiana, P. Sabiniana, Sequoia gigantea, Carpenteria californica, Jamesia americana californica, Staphylea Bolanderi, Rhamnus Purshiana anonaefolia, R. rubra, Ceanothus Lemmonii* and *Fremontia californica.*

Columbia Area. This comprises the valley of the middle portion of the Columbia River and the lower portions of its tributaries, chief of which are the Snake, Yakima, John Day and Deschutes.

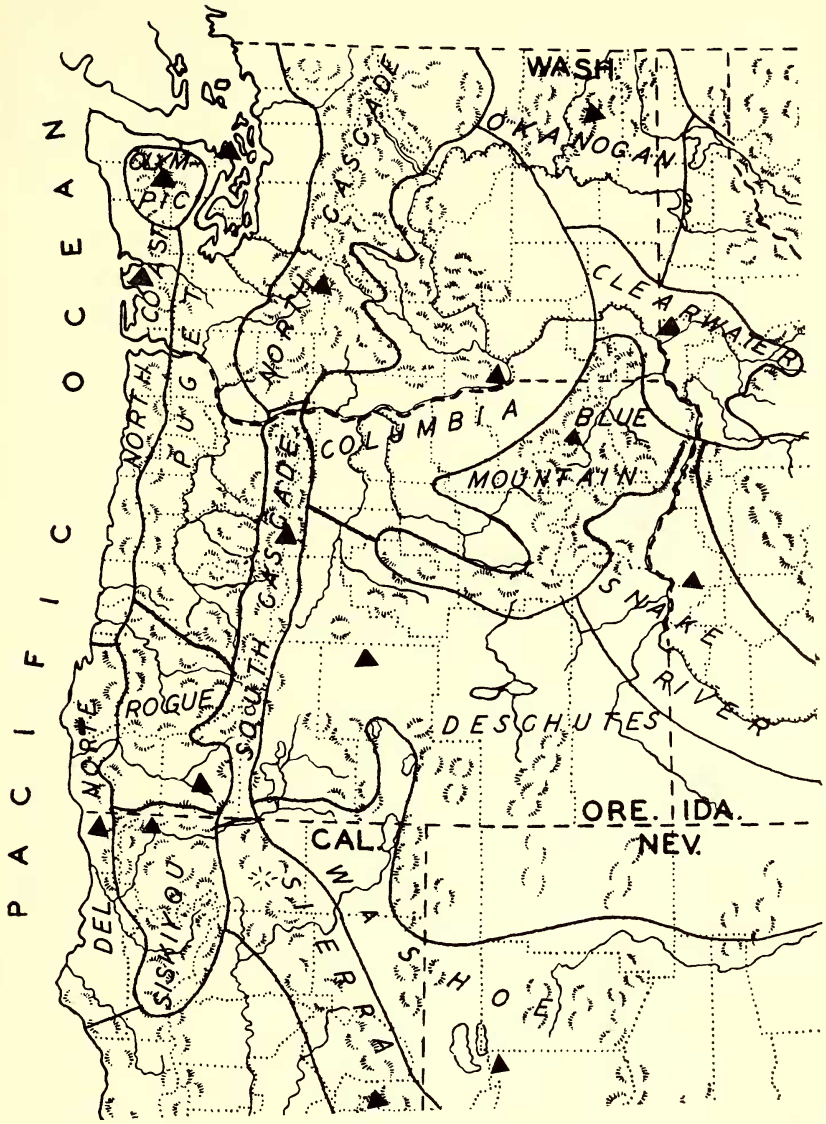

Fig. 6. Vegetation areas of the Pacific Northwest. Triangles indicate the centers of environmental extremes.

Its low precipitation, high summer and relatively high winter temperatures and long growing season are extremes of climatic gradients whose opposite extremes are in the Cascade Mountains, Blue Mountains and Okanogan Highlands, which together roughly surround the area. The region is primarily grassland, with sage-

brush keenly competing with the grasses. Characteristic species are *Agropyron spicatum, Poa secunda* and *Artemisia tridentata.* In the more alkaline situations *Elymus glauca* and *Sarcobatus vermiculatus* are common. Along streams and in the canyons some of the species which mark the vegetation of this area are *Rhus glabra occidentalis, R. Toxicodendron* and *Prunus demissa.*

Clearwater Area. Centered in the lower valley of the Clearwater River in Idaho, with its extremes of low rainfall, high summer and winter temperatures and long growing season, this area extends up the valleys of the Clearwater and its tributaries and out over the rolling hills of southeastern Washington. Its vegetation is typically a bunchgrass association like that of the Columbia Area to the west. The hills and lower mountains within its eastern limits support a forest of *Pinus contorta Murrayana, P. monticola, P. ponderosa* and *Pseudotsuga taxifolia.* No strictly endemic species appears to be sufficiently prominent to serve as a marker for the area, although a number of endemic species occur locally.

Deschutes Area. This area, occupying the extreme northern portion of the Great Basin and the plateau region immediately adjacent to it presents, with a few local exceptions, a fairly uniform set of environmental conditions extending over a considerable territory. The climatic extremes featuring the area are low precipitation, low winter temperature and short growing season, but with no marked extreme of summer temperature. The vegetation is basically a desert shrub formation consisting of *Artemisia tridentata, Chrysothamnus spp.,* and in the more alkaline localities *Sarcobatus vermiculatus, Grayia spinosa, Eurotia lanata, Kochia vestita* and various species of *Atriplex.* Arborescent species frequently occupying slopes and some of the higher elevations are *Juniperus occidentalis, Pinus ponderosa* and *P. contorta Murrayana.*

Snake River Area. The climatic center of this area, located along the Snake River in Washington County, Idaho, and Baker County, Oregon, differs from that of the adjacent Deschutes Area in its high winter and summer temperatures and long growing season. The general character of the vegetation, especially as it extends up the Snake River Valley across southern Idaho, is strikingly similar to that of the sagebrush plains of the Deschutes Area, and the species listed as characterizing the latter might be repeated for the region under discussion. However, especially in its northern extremity in the vicinity of its climatic center, endemic species or subspecies of more local distribution occur with sufficient frequency to emphasize the distinctiveness of its flora.

Washoe Area. The Washoe Area occupies that portion of the Great Basin lying just to the south of the Deschutes Area. Its climatic extremes, viz., low precipitation, high summer and winter temperatures and long growing season, are centered in the Pyra-

mid Lake Valley of western Nevada. The characteristic vegetation of this area is again desert shrub, and the species comprising this formation are largely the same as those in the Deschutes Area. However, the *Juniperus occidentalis* of the latter is here replaced by *J. utahensis* and *Pinus monophylla,* while other species distinguishing the Washoe Area include *Ephedra spp., Celtis Douglasii* and *Prunus Andersonii.*

Blue Mountain Area. The high precipitation, low summer and winter temperatures and short growing season of this elevated area represent the extremes of climatic gradients extending out into the valleys of the Columbia River to the northwest and the Snake River to the east and south. The lower levels of the climatic gradients are occupied by a forest of *Pinus ponderosa* associated with an undergrowth of *Ceanothus velutinus.* This forest is replaced toward the opposite extremes by *Pinus contorta Murrayana, Larix occidentalis, Abies grandis* and *Pseudotsuga taxifolia.* The Blue Mountain Area holds many species in common with the Rocky Mountains, but at the same time is characterized by the occurrence of many endemics.

Okanogan Area. This comprises largely the mountainous region of northeastern Washington known as the Okanogan Highlands, with its extremes of high precipitation, low summer and winter temperatures and short growing season. The southern margin of the area, representing its lower environmental levels, is given over to a grassland formation similar in composition to the grasslands of the Columbia Area. Going toward the environmental center in the higher mountains the vegetation type changes progressively to forests of *Pinus ponderosa, Pseudotsuga taxifolia, Larix occidentalis, Pinus contorta Murrayana, Thuja plicata, Picea Engelmannii* and *Pinus monticola.* The area is also marked by the occurrence of *Juniperus scopulorum, Betula papyrifera occidentalis, Populus tremuloides aurea, Acer Douglasii, Ceanothus sanguineus, C. velutinus* and *Rhus glabra occidentalis.*

Areal Distribution in a Few Pacific Northwest Genera

That the areas delimited in the manner previously shown do constitute centers of endemism is indicated in the work of recent writers who have monographed plant genera or sections of genera which are well represented in the Pacific Northwest. An analysis of these monographs reveals that a relatively large number of species or subspecies are confined wholly or largely to a single area as here treated. A random selection from the monographs is presented in the following table, in which the first column indicates the number of species or subspecies occurring in the Pacific Northwest, and the second column the number of these which are endemic to one area. These endemics are then listed by name and their distribution indicated. Besides the species reported as

TABLE 1. AREAL DISTRIBUTION IN A FEW PACIFIC NORTHWEST GENERA

Total	Endemic		Del Norte	N. Coast	Olympic	Puget	Rogue	Siskiyou	N. Cascade	S. Cascade	Sierra	Columbia	Clearwater	Deschutes	Snake	Washoe	Blue Mts.	Okanogan
3	1	Tofieldia																
		glutinosa absoma																x
11	7	Camassia																
		Quamash maxima				x												
		Quamash azurea				x												
		Howellii					x											
		Quamash intermedia					x											
		Quamash Walpolei					x											
		Quamash utahensis													x			
		Cusickii													x			
15	6	Erythronium																
		Howellii					x											
		oregonum leucandrum					x											
		purpurascens									x							
		tuolumnense									x							
		multiscapoideum									x							
		grandiflorum chrysandrum											x					
24	14	Calochortus																
		uniflorus					x											
		Howellii					x											
		Greenei						x										
		persistens						x										
		monanthus						x										

TABLE 1. (*Continued*)

Total	Endemic		Del Norte	N. Coast	Olympic	Puget	Rogue	Siskiyou	N. Cascade	S. Cascade	Sierra	Columbia	Clearwater	Deschutes	Snake	Washoe	Blue Mts.	Okanogan
Calochortus—(*Continued*)																		
		Lyallii							x									
		minimus									x							
		superbus									x							
		monophyllus									x							
		coeruleus									x							
		Douglasianus											x					
		macrocarpus maculosus											x					
		nitidus															x	
		apiculatus																x
29	13	Arabis																
		furcata olympica			x													
		furcata purpurascens					x											
		Koehleri					x											
		subpinnatifida					x											
		Breweri						x										
		lyrata occidentalis							x									
		Holboellii							x									
		suffrutescens horizontalis								x								
		Whitedii										x						
		Nuttallii										x						
		Cusickii										x						
		sparsiflora atrorubens										x						
		puberula												x				

TABLE 1. (*Concluded*)

Total	Endemic		Del Norte	N. Coast	Olympic	Puget	Rogue	Siskiyou	N. Cascade	S. Cascade	Sierra	Columbia	Clearwater	Deschutes	Snake	Washoe	Blue Mts.	Okanogan
8	4	Sedum																
		laxum latifolium	x															
		laxum typicum					x											
		obtusatum boreale						x										
		obtusatum typicum									x							
30	15	Penstemon																
		Rattanii typicus	x															
		hesperius				x												
		ovatus				x												
		anguineus						x										
		washingtonensis							x									
		Peckii							x									
		heterodoxus typicus									x							
		heterodoxus cephalophorus									x							
		shastensis									x							
		Vaseyanus										x						
		subserratus										x						
		glaucinus												x				
		attenuatus palustris															x	
		spathulatus															x	
		elegantulus															x	
5	2	Wyethia																
		helenioides									x							
		helianthoides															x	

endemic to one area only, there are others which occur in two or three areas only, these areas being similar as to climatic extremes.

The genera and their monographers herein referred to are the following: *Tofieldia,* Hitchcock (1944); *Camassia,* Gould (1942); *Erythronium,* Applegate (1935); *Calochortus,* Ownbey (1940); *Arabis,* Rollins (1936); *Sedum,* Clausen (1942); *Penstemon,* Keck (1945); *Wyethia,* Weber (1946).

Summary

In any region extensive enough to show physiographic variability, the climatic or other environmental factors occur as gradients. Previous investigation has shown that where several extremes of these gradients occur together they mark the center of an area rich in endemic plant species. In this study the Pacific Northwest has been divided into sixteen vegetation areas, each built around one of these centers of environmental extremes. Each area is briefly characterized as to its dominant plant association. Examples from the recent works of monographers show how the distribution of most plant species fits into the pattern of these areas.

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